# EDIACARAN BIOTA OF THE WERNECKE MOUNTAINS, YUKON, CANADA

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ABSTRACT. Soft-bodied metazoans, trace fossils, and metaphytes occur throughout several hundred metres of post-tillite, pre-Cambrian strata in the Wernecke Mountains, east-central Yukon Territory. The fossils occur in three unnamed units of siltstone deposited under shallow shelf and deeper water conditions. The oldest fossiliferous unit, the 'Goz siltstone', contains *Charniodiscus*? and *Cyclomedusa* sp. Siltstone unit 2 has yielded macrofossils (*Beltanelliformis brunsae*, *Medusinites asteroides*, *Rugoconites*? sp.), trace fossils (*Planolites montanus*), and carbonaceous compressions (*Vendotaenia*? sp.). Siltstone unit 1, the youngest of the three siltstones, exhibits abundant soft-bodied macrofossils (*Beltanella gilesi*, *Beltanelliformis brunsae*, *Charniodiscus* cf. *arboreus*, *Cyclomedusa plana*, *C.* sp., Ediacaria flindersi, Kullingia? sp., *Medusinites asteroides*, *Nadalina yukonenis* gen. et sp. nov., *Spriggia annulata*, *S. wadeae*, *Tirasiana* sp.) and trace fossils (*Gordia marina*, *Neonereites*? sp., *Planolites montanus*, and a backfilled burrow). Overlying Proterozoic carbonates contain only simple trace fossils.

The Wernecke assemblage is similar to other occurrences of the Ediacaran fauna, but is most closely comparable with the Valday assemblage of the Russian Platform and the type assemblage in South Australia. Similarity of the faunal sequence in the Wernecke Mountains with that present in the type Ediacaran and Vendian implies that evolutionary stages previously identified within these systems may be globally significant.

THE Ediacaran fauna is a distinctive assemblage of soft-bodied metazoans and simple trace fossils that occurs above the highest Varangian tillites and below the lowest fossiliferous deposits of the Cambrian (see Glaessner 1984 and references therein). This fossil assemblage has been reported from every continent except Antarctica (Glaessner 1984, Fig. 1/8), and is particularly well developed in Australia, Namibia, Newfoundland, and the Russian Platform. The widespread occurrence of this distinctive assemblage has supported calls for recognition of a formal, sub-Cambrian geological period, variously termed the Vendian (Sokolov 1952; Sokolov and Fedonkin 1984), Ediacaran (Jenkins 1981), Ediacarian (Cloud and Glaessner 1982), or Sinian (Grabau 1922; Xing 1984). While all have 'the base of the Cambrian' as their common upper limit, none of these proposed formal units has the same lower limit. A discussion of the relative merits of each is beyond the scope of the present paper. However, for the purposes of this paper we prefer to use Ediacaran for the shortest interval with soft-bodied fossil assemblages, because the first *diverse* assemblage to be described and used for comparison derives from the Ediacara Hills region in South Australia. The faunally characterized Ediacaran is encompassed chronologically by the longer Vendian interval (and the Vendian by the still longer Sinian).

Elements of the Ediacaran fauna were first discovered in the Wernecke Mountains (text-fig. 1) during a reconnaissance geologic study by Fritz *et al.* (1983). Their collection included the trace fossils *Gordia* sp. and *Palaeophycus tubularis* Hall (Fritz *et al.* 1983; Nowlan *et al.* 1985), and the macrofossils *Cyclomedusa davidi*? Sprigg and *Beltanelliformis brunsae* Menner (Hofmann *et al.* 1983); Hofmann (1984) subsequently described microfossils from these samples. During the summer of 1984, the present authors carried out more detailed geological studies (Narbonne *et al.* 1985), collecting numerous fossil specimens from three unnamed formations. These specimens help to elucidate the taxonomy, palaeoecology, and palaeogeography of early metazoans, and also aid in the regional and global correlation of the fossil-bearing strata.

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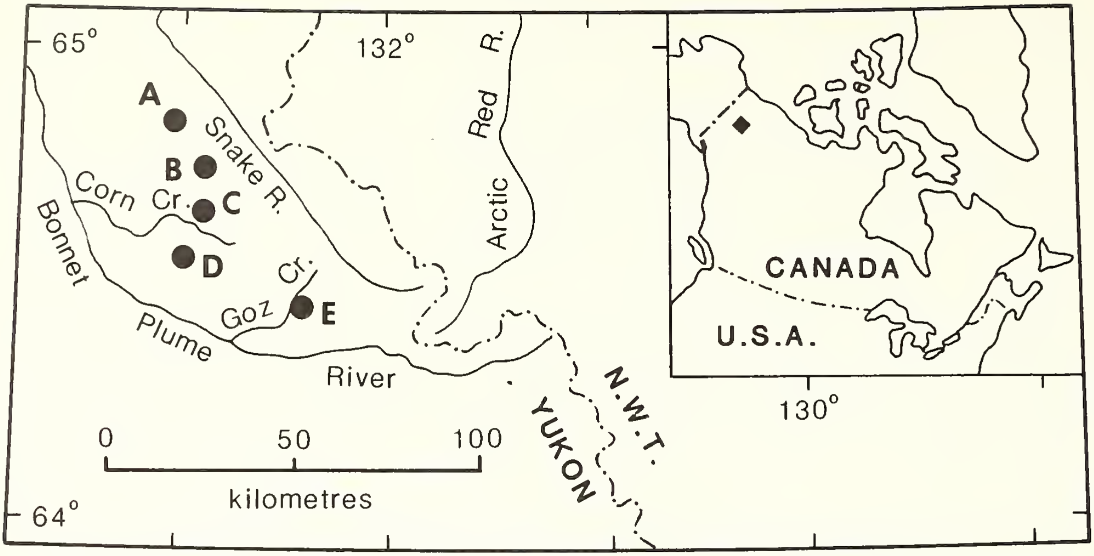


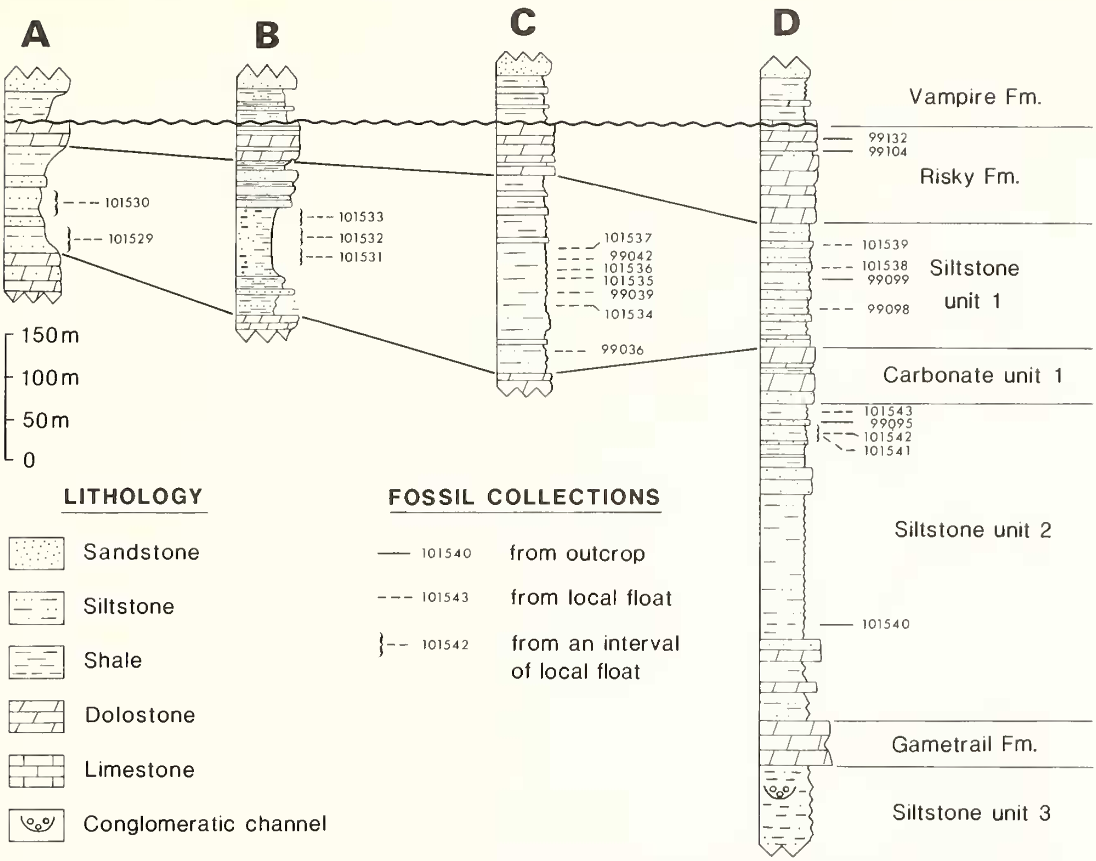

TEXT-FIG. 1. Index map showing location of sections studied in the eastern Wernecke Mountains.

## GEOLOGICAL SETTING AND AGE

The Wernecke Mountains lie on the southern edge of the Yukon Stable Block (Lenz 1972), a site of predominantly shallow-water sedimentation throughout most of the late Proterozoic and early Palaeozoic. To the south, the strata pass into deeper-water shales and turbiditic conglomerates (Gordey 1980; Cecile 1982).

The strata considered in this study occur in equivalents to the upper part of the Windermere Supergroup, a predominantly clastic succession that can be traced throughout the Canadian Cordillera (Eisbacher 1981). The base of the Windermere Supergroup is younger than 770 Ma (Park and Aitken 1986) and probably younger than 730 Ma (Evenchick *et al.* 1984); its top is located at the base of the lowest Cambrian unit (Eisbacher 1981). Ediacaran macrofossils occur in the upper part of the Windermere Supergroup in southern British Columbia (Hofmann *et al.* 1985), western Northwest Territories (Hofmann 1981) and eastern Yukon Territory (Hofmann *et al.* 1983; this study). The Windermere Supergroup in the study area is more than 2 km thick, and exhibits glacial and glaciomarine deposits possibly equivalent to the Sturtian and Marinoan glaciations in its lower half (Eisbacher 1985). The Windermere Supergroup is disconformably overlain by the Vampire Formation (text-fig. 2), which contains, in its basal beds, small shelly fossils including *Anabarites trisulcatus* and *Protohertzina anabarica*; Nowlan *et al.* (1985) regarded this fauna as correlative with the *Anabarites–Circotheca–Protohertzina* Assemblage Zone of south-western China and with the Nemakit-Daldyn Horizon of Siberia, both of which would be placed immediately below the base of the Cambrian if the proposed base in Yunnan, China is accepted (Cowie 1985). Trace fossils in the same beds include two genera of arthropod burrows (*Rusophycus* and *Cruziana*) generally regarded as Cambrian or younger in age (Nowlan *et al.* 1985; Narbonne *et al.* 1987). The Vampire Formation is conformably overlain by the Sekwi Formation, a Lower Cambrian carbonate unit containing trilobites of the *Fallotaspis* and *Nevadella* zones near its base (Fritz 1978). Thus, the units bearing the fauna reported here occur stratigraphically between late Proterozoic glacial deposits and fossiliferous Lower Cambrian strata, and can therefore be regarded as Ediacaran in age.

Ediacaran strata in the study area comprise a succession of alternating carbonate and fine siliciclastic units, with soft-bodied macrofossils recognized only in the siliciclastic units (Narbonne *et al.* 1985). Due to the reconnaissance level of geological study, formal stratigraphic names have not yet been proposed for most of these units nor can the palaeoecology be discussed in detail. This paper




TEXT-FIG. 2. Stratigraphic sections with collection localities (Geological Survey of Canada [GSC] numbers). Sections A, D from Narbonne *et al.* (1985), Section B from Aitken (1984), Section C from Fritz *et al.* (1983). Risky Formation (Aitken, in press) = map unit 11 of Blusson (1971).

will use the names suggested by Fritz *et al.* (1983), Fritz (1984), Aitken (1984), Narbonne *et al.* (1985), and Aitken (in press).

The oldest unit containing macrofossils is the 'Goz siltstone', which crops out on Goz Creek at locality 'E' (text-fig. 1). The 'Goz siltstone' occurs as a small, isolated fault block; it cannot be directly correlated with any unit in sections A–D, but is lithologically similar to Siltstone unit 3 at locality 'D' and the Sheepbed Formation of the western Northwest Territories (Narbonne *et al.* 1985). The 'Goz siltstone' consists predominantly of thin- to medium-bedded siltstone. Slump and load structures are common; ripple-marks are very rare. Granule-filled channels averaging 0·5 m deep occur sporadically. Most channels are filled with clast-supported, normally graded material, but some contain matrix-supported, massive fill. These features, combined with the apparent absence of structures typical of shallow-water conditions, suggest that deposition occurred on a slope in a deeper-water setting. Macrofossils occur on bedding surfaces in the siltstone.

Siltstone unit 2 at locality 'D' (text-figs. 1 and 2) consists predominantly of recessive-weathering shale and siltstone with sporadic interbeds of quartzose sandstone and minor dolostone. Individual sandstone beds are very thin and graded, and most likely represent storm deposits. The upper part of the unit has several laterally discontinuous, coarsening-upwards sandstone packages up to 8 m thick; lower parts of the cycles are characterized by planar–tabular and hummocky cross-stratification, and the upper parts of cycles exhibit sporadic desiccation cracks. Deposition probably occurred on a wave- or storm-dominated shelf, with the coarsening-upwards sandstones representing sand bars. Carbonaceous remains of metaphytes occur in dark-grey shale in the lower part of the unit (GSC loc. 101540), whereas metazoans and trace fossils occur as positive features on the soles of very thin to thin, storm-deposited sandstone beds near the top of the unit (text-fig. 2).

Siltstone unit 1 crops out at localities 'A' to 'D' (text-figs. 1 and 2). It is lithologically similar to Siltstone unit 2, differing mainly in that the thick sandstone beds are more continuous laterally. Synaeresis cracks are abundant, but desiccation cracks were not observed. Deposition probably occurred on a wave- or storm-dominated shelf. Macrofossils are found sporadically throughout the lower two-thirds of the unit; trace fossils occur rarely in the lower half of the unit but are common throughout the upper half. Macrofossils and trace fossils are seen chiefly as positive features on the soles of very thin to thin, storm-deposited sandstone beds; only very rarely are they preserved as negative features on the tops of these beds. No slabs exhibiting both macrofossils and trace fossils were observed.

These occurrences suggest that the Ediacaran organisms preserved in Siltstone units 1 and 2 lived in a shallow sublittoral environment, whereas those present in the 'Goz siltstone' lived in a deeper-water environment. This is consistent with other reports of the Ediacaran fauna, which are from both shallow shelf (e.g. Goldring and Curnow 1967; Jenkins *et al.* 1983) and deeper slope (e.g. Anderson and Conway Morris 1982; Gibson *et al.* 1984) settings.

## BIOSTRATIGRAPHY

As now known, the Ediacaran macrobiota of the Wernecke Mountains comprises an assemblage of 14 species of metazoan fossils (one of which is new), 1 metaphyte, and 5 trace fossils. In addition, 3 dubiofossils are reported. The greatest taxonomic diversity is exhibited by soft-bodied discoidal structures: 11 of the 14 species can be broadly referred to 9 'medusoid' genera; one species is a pennate coelenterate, and one is a possible organ of attachment to the substrate. The numerically dominant soft-bodied organism in the assemblage is a gregarious species of compressed globular structures assigned to *Beltanelliformis brunsae*. In addition, 5 species of ichnofossils characterize the upper part of the sequence studied. Of these ichnofossils, only *Planolites montanus* is common.

The Ediacaran fauna of the Wernecke Mountains is considerably more diverse than that reported from map-unit 10B of the Mackenzie Mountains of the western Northwest Territories by Hofmann (1981). However, the presence of *B. brunsae* and *Gordia marina* in both areas is consistent with lithostratigraphic evidence (Fritz *et al.* 1983; Aitken, in press) that the strata are equivalent.

The Wernecke assemblage is broadly similar to Ediacaran assemblages reported from other areas, particularly Australia and Eurasia (text-fig. 3). Similarity of the Wernecke assemblage to Ediacaran/Vendian assemblages from Australia, the Russian Platform, Siberia, China, England, Newfoundland, and several other localities supports recent calls (e.g. Jenkins 1981; Cloud and Glaessner 1982; Sokolov and Fedonkin 1984) for recognition of a formal geological period based on this fauna.

Although many authors believe that several biostratigraphic zones can be recognized within the Ediacaran/Vendian, intercontinental correlation of these macrofossil zones has proved difficult. The Vendian of the Russian Platform can be divided into four zones which Sokolov and Fedonkin (1984) considered to be stages. The global applicability of these 'zones' or 'stages' is currently uncertain (see Jenkins 1981, p. 181 and references therein). Nevertheless, there would appear to be a close correlation between the faunal sequences of the Wernecke Mountains and the Russian Platform (text-fig. 4).

The basal, Volhyn 'Series' contains deposits of the Varangian glaciation, but apparently lacks macrofossils and trace fossils (Sokolov and Fedonkin 1984). This is most likely equivalent to strata below the fossiliferous units discussed in this paper, which contain glacial deposits and apparently lack macrofossils and trace fossils (Eisbacher 1981). Intercontinental correlation of glacial deposits in the Windermere Supergroup has been discussed by Eisbacher (1985), who recognized equivalents of the Sturtian and Marinoan (= Varangian) glaciations in these strata.

The overlying Redkino 'Series', represented by the Mogilev, Yaryshev, and Nagoriany Formations in the Ukraine and by the Pletevev and Ust-Pinega Formations in the Baltic region, contains a diverse

SYNOPSIS OF WERNECKE MOUNTAINS MACROBIOTA

| TAXA (UNITS) | Map unit 11 | | Siltstone unit 1 | | | | | | | | | | | | | | | | Siltstone unit 2 | | | | | Goz siltstone | | | Vendian, Eurasia | Ediacaran, Australia |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SECTIONS | D | | A | | B | | | C | | | | | | | D | | | | | | | | | E | | | | |
| GSC localities | 99132 | 99104 | 101530 | 101529 | 101533 | 101532 | 101531 | 101537 | 99042 | 101536 | 101535 | 99039 | 101534 | 99036 | 101539 | 101538 | 99099 | 99098 | 101543 | 99095 | 101542 | 101541 | 101540 | 101546 | 101545 | 101544 | | |
| Phylum COELENTERATA | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Beltanella gilesi* Sprigg, 1947 | | | | | | | ○ | | | | | | ○ | | | | | | | | | | | | | | ◇ | ◇ |
| *Charniodiscus* cf. *C. arboreus* (Gl. in Gl. & D., 1959) | | | | ○ | | | | | | | | | | | | | | | | | | | | | | | | □ |
| *C.?* sp. | | | | | | | | | | | | | | | | | | | | | | | | | ○ | | □ | □ |
| *Cyclomedusa plana* Gloessner & Wade, 1966 | | | | | | | | | | | ○ | | | | | | | | | | | | | | | | ◇ | ◇ |
| *C.* sp. | | | | | | | ○ | ○ | ○ | | | ○ | | | | | | | | | | | | ○ | | ○ | □ | □ |
| *Ediacaria flindersi* Sprigg, 1947 | | | | | | ○ | | | | | | | | | | | | | | | | | | | | | ◇ | ◇ |
| *Kullingia?* sp. | | | | | | | | | | | | | ○ | | | | | | | | | | | | | | □ | □ |
| *Medusinites asteroides* (Sprigg) Gl. & W., 1966 | | | | | | | | | ○ | ○ | | | | | | | | | | ○ | | | | | | | ◇ | ◇ |
| *Nadalina yukonensis* gen. et sp. nov. | | | | | | | | | | | | | | | | ○ | | | | | | | | | | | | |
| *Rugoconites?* sp. | | | | | | | | | | | | | | | | | | | | | | ○ | | | | | | □ |
| *Spriggia annulata* (Sprigg) Southcott, 1958 | | | ○ | | | | | | | | | | | | | | | | | | | | | | | | □ | ◇ |
| *S. wadeae* Sun, 1986 | | | | | | | | | | | | | ○ | | | | | | | | | | | | | | □ | ◇ |
| *Tirasiana* sp. | | | | | | | ○ | | ○ | | | | | | | | | | | | | | | | | | ◇ | □ |
| Phylum uncertain | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Beltanelliformis brunsae* Menner, 1974 | | | ○ | ○ | | ○ | ○ | | ○ | | | ○ | ○ | ○ | | | | | ○ | ○ | ○ | ○ | | | | | ◇ | □ |
| ICHNOFOSSILS | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Gordia marina* Emmons, 1844 | | | | | ○ | | | | | | | | | | | | | ○ | | | | | | | | | ◇ | |
| *Neonereites?* sp. | | | | | ○ | | | | | | | | | | | | | | | | | | | | | | □ | |
| *Palaeophycus tubularis* Hall, 1847 | △ | △ | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Planolites montanus* Richter, 1937 | | | ○ | | ○ | ○ | ○ | | ○ | ○ | | | | | ○ | | ○ | | | | | ○ | | | | | ◇ | ◇ |
| Backfilled burrow | | | | | | ○ | | | | | | | | | | | | | | | | | | | | | | |
| Group VENDOTAENIDES Gnilovskoyo, 1971 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Vendotaenia?* sp. | | | | | | | | | | | | | | | | | | | | | | | ○ | | | | □ | |
| DUBIOFOSSILS | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Dubiofossil A | | | | | | | | | | ○ | | | | | | | | | | | | | | | | | | |
| Dubiofossil B | | | | | | ○ | | | | | | | | | | | | | | | | | | | | | | |
| Dubiofossil C | | | | | | | | | | | | | | | | | | | | | | ○ | | | | | | |

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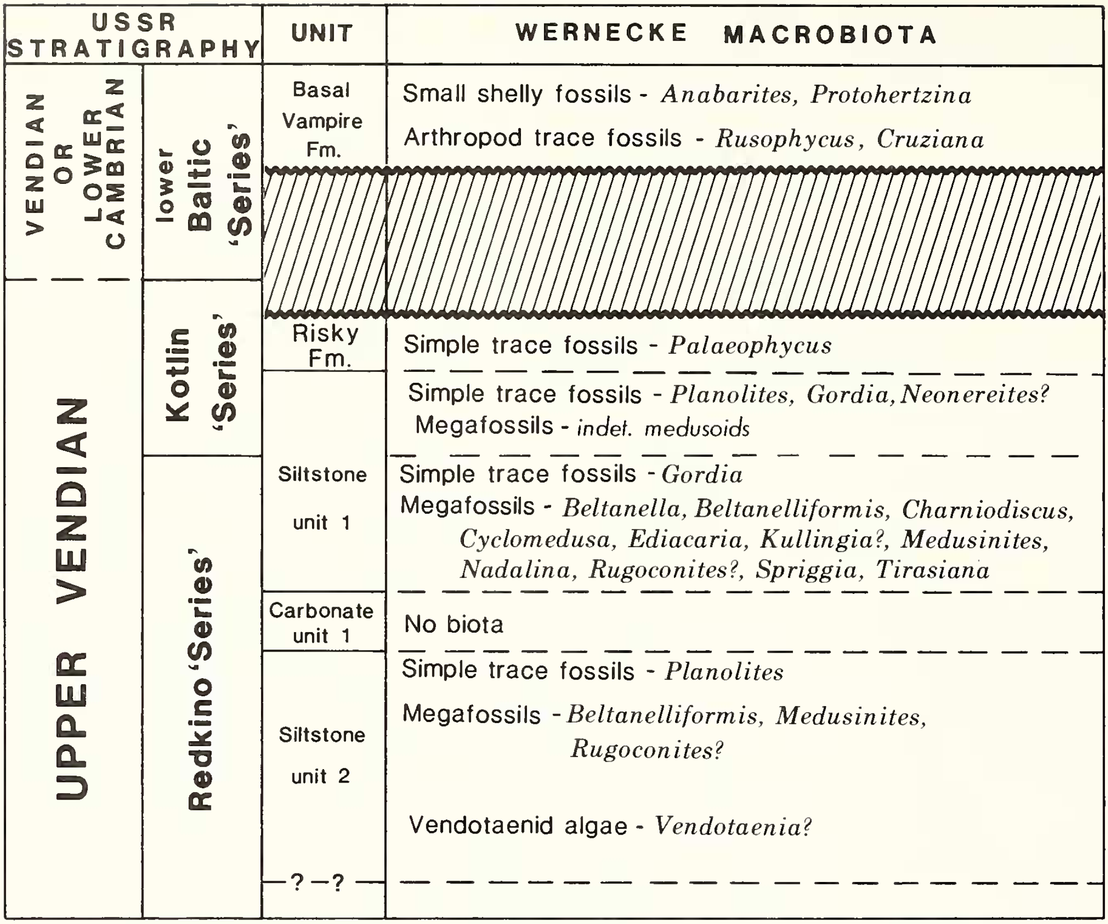
TEXT-FIG. 3. Synopsis of Ediacaran macrobiota of Wernecke Mountains. Specimens from the present study are shown by circles; triangles identify specimens described by Nowlan *et al.* (1985) from map-unit 11 (= Risky Formation). For comparison, same (rhombs) or similar (squares) forms from Australia and Eurasia are also indicated.

assemblage of soft-bodied metazoans along with vendotaenid algae and simple trace fossils (Palij *et al.* 1979; Sokolov and Fedonkin 1984). This is similar to the 'Goz siltstone', Siltstone unit 2, and the lower two-thirds of Siltstone unit 1, which contain a similar assemblage. Indeed, most of the specific forms found in these three units have also been described from the type Redkino 'Series' (text-fig. 3).

The overlying Kotlin has yielded vendotaenid algae and simple trace fossils, but only sparse 'medusoids' (Palij *et al.* 1979; Sokolov and Fedonkin 1984). This compares with the upper third of Siltstone unit 1 and all of the Risky Formation (= map-unit 11 of Blusson 1971; see Aitken, in




TEXT-FIG. 4. Proposed correlation of the upper part of the Windermere Supergroup with the Vendian of the Russian Platform. Similar correlations can be made with the Ediacaran of Australia.

press), which exhibit simple trace fossils and sparse, predominantly indeterminate 'medusoids'. Both in the Russian Platform and in the Wernecke Mountains, this zone contains relatively few diagnostic taxa, and is recognized primarily by its position between the more distinctive fossil assemblages of the overlying and underlying strata.

Overlying the Kotlin 'Series' on the Russian Platform is the Baltic 'Series'. This 'series' traditionally has been regarded as Lower Cambrian (e.g. Sokolov 1973; Palij *et al.* 1979), but recently some authors (e.g. Sokolov and Fedonkin 1984) have included its basal 'horizon', the Rovno, in the upper Vendian. The small shelly fossil assemblage of the basal Vampire Formation is broadly similar to that of the Nemakit-Daldyn (Nowlan *et al.* 1985), which Sokolov and Fedonkin (1984) regarded as the Siberian equivalent of the Rovno 'Horizon'. However, the abundance of arthropod traces (*Rusophycus, Cruziana*) in the basal Vampire suggests that correlation with the Lontova 'Horizon', which immediately overlies the Rovno on the Russian Platform, is more probable. The Lontova 'Horizon' is also part of the lower Baltic 'Series', and is generally regarded as Lower Cambrian (e.g. Fedonkin 1985*b*).

Similar correlations can be made with the Ediacaran of South Australia (Jenkins 1981). Marinoan (= Varangian) glaciomarine deposits occur at the top of the Umberatana Group (Coats 1981), and have been correlated with probable glacial deposits in the middle part of the Windermere Supergroup by Eisbacher (1985). Problematic remains of Ediacaran aspect occur sporadically throughout the lower part of the overlying Wilpena Group (Cloud and Glaessner 1982, fig. 2F; Dyson 1985), and a diverse Ediacaran assemblage is present in the upper part of the Wilpena Group (Pound Subgroup). The macrofossil assemblage of the Pound Subgroup is closely similar to that of the Wernecke Mountains (text-fig. 3) and the Redkino 'Series' of the Russian Platform (Jenkins 1981; Cloud and Glaessner 1982; Sokolov and Fedonkin 1984), thereby implying that the strata are equivalent. The Pound Subgroup is disconformably overlain by the Uratanna Formation, which contains Cambrian trace fossils near its top (Daily 1972, 1973).

Similarity of the faunal and floral sequence between the Wernecke Mountains, the Russian Platform, and the Adelaide Geosyncline suggests that intercontinental correlation of stages and even zones may be possible within the Ediacaran/Vendian.

## SYSTEMATIC PALAEONTOLOGY

The taxonomic affinities of the Ediacaran fauna are currently controversial. Until recently, most authors followed Sprigg (1949), Richter (1955), and Glaessner (1979, 1984) in regarding most discoid and pennate forms as the impressions of fossil coelenterates. Seilacher (1984) and McMenamin (1986) have questioned this interpretation, suggesting that some of these fossils may represent radial or circular burrows, internal sandy skeletons, or representatives of an extinct phylum. A full evaluation of the affinities of the Ediacaran fauna is beyond the scope of this paper and we have tentatively followed the *Treatise* (Glaessner 1979) in referring most of our taxa to the Coelenterata (text-fig. 3).

In the following section, synonymies include only putative pre-Cambrian occurrences. An alphabetical list for each major group of the Ediacaran biota of the Wernecke Mountains, and their stratigraphic and geographic distributions, is shown in text-fig. 3. Terminology regarding preservation follows Frey (1973, table 5).

All figured specimens are in the repository of the National Type Collection of Invertebrate and Plant Fossils (GSC) in Ottawa.

### Phylum COELENTERATA
### Genus BELTANELLA Sprigg, 1947

*Type species*. *Beltanella gilesi* Sprigg, 1947.

### *Beltanella gilesi*

Plate 73, fig. 6

For synonymy up to 1966, see Glaessner and Wade (1966).

1972*a* *Planomedusites grandis* Sokolov, pl. 2, fig. 1.
1973 *Planomedusites grandis* Sokolov, p. 210, fig. 3/1.
1979 *Planomedusites grandis* Glaessner, p. A96, fig. 10/3.

*Description*. Smooth disc with narrow raised rim; two specimens preserved in convex hyporelief, respectively 36 and 46 mm in diameter and 1·5 mm and 1·7 mm in maximum relief; smaller specimen with central protruberance 3 mm across, partly enclosed by low concentric ridge 9 mm in diameter; larger specimen exfoliated and incomplete; both specimens surrounded by a flange about 2·5 mm wide.

*Remarks*. Our structures strongly resemble the holotype of *B. gilesi* Sprigg, which, however, has uniformly sized and equidistantly spaced circular markings at two-thirds the distance to the margin, as well as radial grooves. Glaessner and Wade (1966) hypothesized that these features might be accidental, a view supported by undescribed new specimens from Australia (R. J. F. Jenkins, pers. comm. 1986). *Beltanella* is similar in size and morphology to *Ediacaria* Sprigg (Glaessner and Wade 1966; Glaessner 1979), but can be distinguished by the presence of an outer flange.

### Genus CHARNIODISCUS Ford, 1958

*Type species. Charniodiscus concentricus* Ford, 1958.

### *Charniodiscus* cf. *arboreus* (Glaessner, 1959)

Text-fig. 5*d*

*Description.* Two incomplete specimens preserved as large, ovate convex hyporeliefs. Larger specimen 98 × 72 mm, with at least 5·6 mm of relief at margin; roughly bilaterally symmetrical impression of flattened, bag-like


TEXT-FIG. 5. Macrofossils from the 'Goz siltstone' and siltstone unit 1. *a*, *Cyclomedusa* sp., epirelief. GSC loc. 101546. GSC 83016, × 1. *b*, *Charniodiscus*? sp., epirelief. GSC loc. 101545. GSC 83017, × 1. *c*, *Charniodiscus* cf. *arboreus* Glaessner. Two incomplete specimens (middle, GSC 83019; upper right, GSC 83020). Hyporelief. GSC loc. 101529, × 1.

body with parallel-sided, regular segments between 7 and 10 mm wide, extending outwards in apparently alternating series, at angles of about 60° with a poorly defined axial region, opening towards the more pointed end of the specimen (distal apex). Segments separated by straight to very slightly curved 1·0–1·5 mm wide furrows and associated one or two juxtaposed low, parallel, levee-like ridges; suggestion of short, oblique secondary furrows directed inward at angles near 40° from main furrows in wider (lower) part of specimen. Apical region subtriangular, concavo-convex, marked by fine wrinkles parallel with concave side of apical region; region 15 mm across immediately below triangular apex marked by delicate concentric wrinkles. Surface of segmented portion with randomly spaced (and probably accidental) subcircular tubercles 0·5–7·0 mm across and up to 1·0 mm of relief. Transverse section across lower end showing two irregular narrow vertical zones marked by mineralogical and textural contrast.

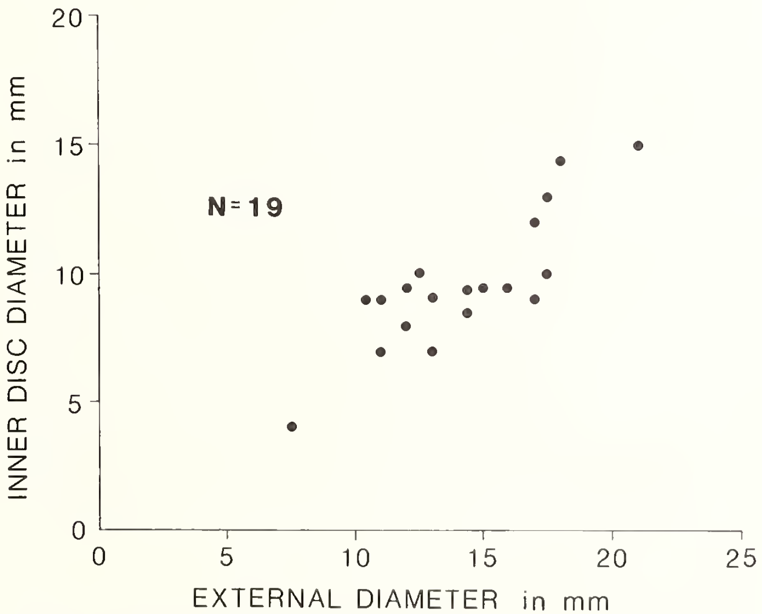
Smaller specimen an ovate hyporelief 50 × 26 mm, 10 mm high; surface bearing transverse convex segments of unequal width, from 6–12 mm wide, separated by pronounced furrows; surface marked by fine, oblique wrinkles continuous across furrows; transverse section showing recurved nature of impression and sedimentary lamination paralleling lower surface of hyporelief.

*Remarks.* The structures are indicative of the organization and highly flexible nature of genera such as *Charniodiscus* and *Inkrylovia*. The larger specimen somewhat resembles the *Rangea arborea* illustrated by Glaessner *in* Glaessner and Daily (1959, pl. 43, figs. 2 and 3; pl. 44, fig. 3; later assigned to *Arborea arborea* [Glaessner and Wade 1966, p. 619], and finally placed in synonymy with *Charniodiscus* [Glaessner 1979, p. A99]), and may represent a partially decomposed and over-folded specimen of this taxon. The smaller specimen has few distinguishing characteristics; its preservation is similar to a specimen referred to *Inkrylovia* from the correlative map-unit 10B in the Mackenzie Mountains 250 km east-south-east (Hofmann 1981, fig. 3A, B).

*Charniodiscus*? sp.

Text-figs. 5*b*, *c* and 6

*Description.* Nineteen specimens occurring as convex epireliefs and concave hyporeliefs at the interface between two very thin beds of siltstone. Bipartite structure, consisting of a rough-textured central disc surrounded by a smooth, flat outer ring with slight (< 0·3 mm) relief. External diameter 7·5–21·0 mm (mean = 14·3 mm); diameter




TEXT-FIG. 6. Size variations in *Charniodiscus*? sp. from the 'Goz Siltstone'.

of the inner disc 4–15 mm (mean = 9·7 mm); diameter of the inner disc 50–90% (average 68%) of the entire fossil (text-fig. 6). Outer margin of the fossil circular to subcircular, with minor indentations (text-fig. 5*c*). Inner disc centrally to slightly eccentrically located. Faint impression of a rod-like stem 2·5–6·0 mm wide attached to the inner disc. Specimens preserved as cleavage reliefs, with no structure visible below or above the bedding surface.

*Remarks*. The apparent absence of vertical tubes below or above the specimens implies that the structures did not form as a result of water or gas escape. Small pyrite concretions approximately one metre lower stratigraphically exhibit a central core of pyrite and an outer ring of darker (reduced) sediment; these can readily be distinguished from *Charniodiscus*? sp. by the fact that the outer ring has a different mineralogy and colour, but no difference in relief. The faint impression of a stem further serves to distinguish *Charniodiscus*? sp. from inorganic sedimentary structures and from medusiform genera with bipartite organization (e.g. *Medusinites* Glaessner and Wade, 1966; *Nimbia* Fedonkin, 1980).

Ford (1958) originally described *Charniodiscus* solely on the basis of its bipartite disc-like structure, but later (1963) figured the entire specimen with the bipartite disc attached by a stem to a frond-like structure. Subsequent workers (e.g. Jenkins and Gehling 1978; Glaessner 1979) have regarded the frond as the diagnostic portion of the organism. The Wernecke specimens exhibit an incomplete stem but lack the attached frond, and hence can only tentatively be referred to *Charniodiscus*.

### Genus CYCLOMEDUSA Sprigg, 1947

*Type species*. *Cyclomedusa davidi* Sprigg, 1947.

### *Cyclomedusa plana* Glaessner and Wade, 1966

Plate 73, fig. 3

1966 *Cyclomedusa plana* Glaessner and Wade, p. 607, pl. 98, figs. 1–3.
1968 *Cyclomedusa plana* Zaika-Novatskiy and Palij, pp. 133–134, fig. 1 (English translation, pp. 269–270, fig. 1).
1973 *Cyclomedusa plana* Sokolov, p. 209, fig. 2/1.
1979 *Cyclomedusa plana* Glaessner, p. A94, fig. 9/2*a*.
? 1981 *Cyclomedusa* cf. *plana*, Fedonkin, pp. 58–59, pl. 2, fig. 1; pl. 3, fig. 4.
? 1983 *Cyclomedusa* cf. *plana*, Fedonkin *in* Velikanov *et al*., pl. 28, fig. 7.
? 1985*a* *Cyclomedusa* cf. *plana* Fedonkin, pp. 71–72, pl. 2, figs. 3 and 5; pl. 5, fig. 7.

*Description*. One partially preserved circular impression (hyporelief) with bipartite organization; inner disc, 24 mm in diameter, with four coarse, slightly eccentric folds; small, bud-like, concentric pattern superimposed

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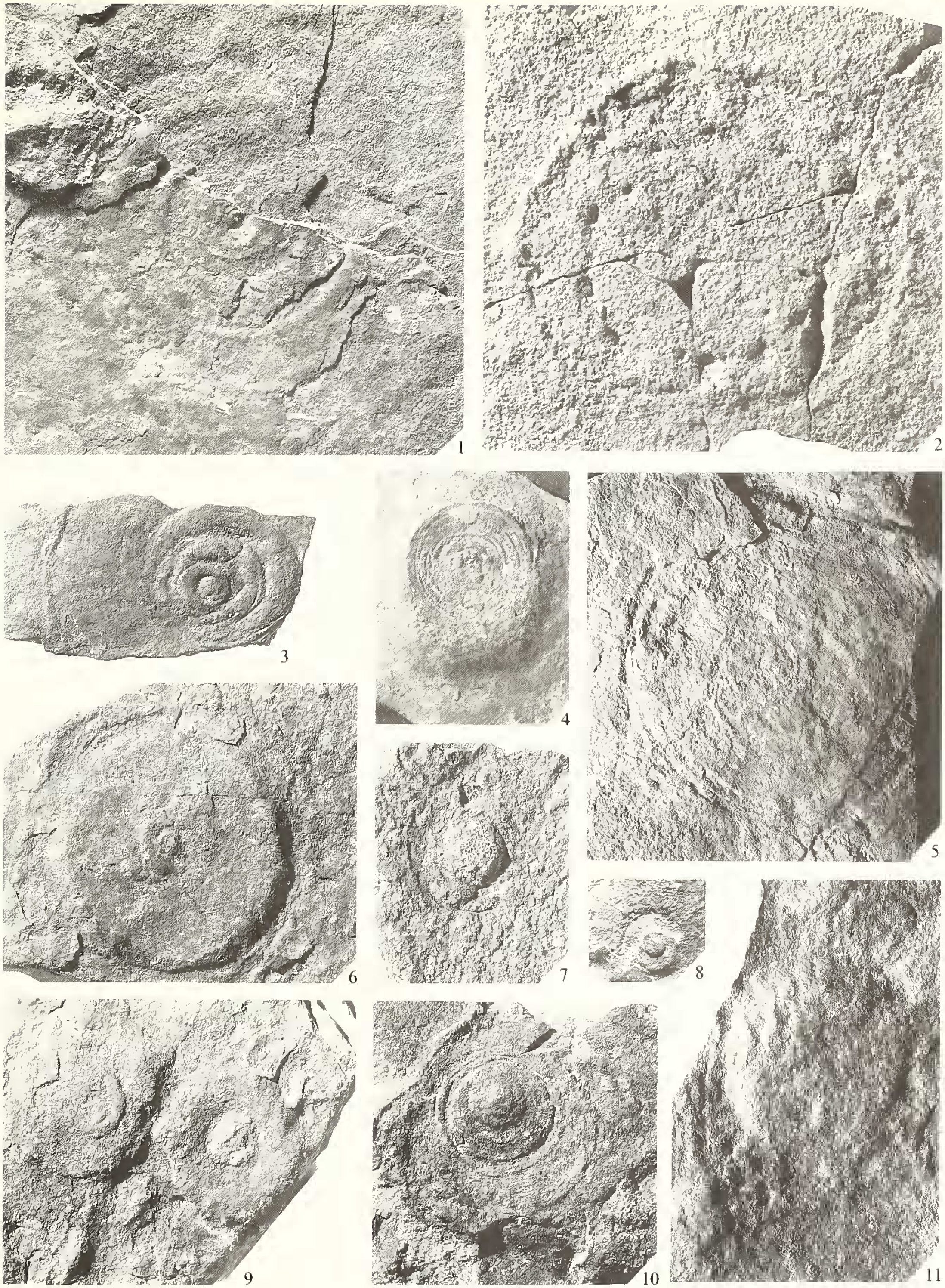
EXPLANATION OF PLATE 73

Fig. 1. *Cyclomedusa* sp. Sprigg. GSC loc. 101537. GSC 83021, ×1.
Fig. 2. *Nadalina yukonensis* gen. et sp. nov., epirelief. Holotype. GSC loc. 101535. GSC 83022, ×1.
Fig. 3. *C. plana* Glaessner and Wade, hyporelief. GSC loc. 101535. GSC 83023, ×1.
Fig. 4. *Spriggia wadeae* Sun, hyporelief. GSC loc. 101534. GSC 83024, ×1.
Fig. 5. *Kullingia*? sp., hyporelief. GSC loc. 101534. GSC 83025, ×1.
Fig. 6. *Beltanella gilesi* Sprigg, hyporelief. GSC loc. 101531. GSC 83026, ×1.
Figs. 7–9. *Medusinites asteroides* (Sprigg), hyporelief. 7, GSC loc. 99095. GSC 83027, ×1; 8, GSC loc. 99042. GSC 83028, ×1; 9, GSC loc. 101536. GSC 83029, ×1.
Fig. 10. *S. annulata* (Sprigg). Specimen on shale pebble. GSC loc. 101530. GSC 83030, ×1.
Fig. 11. *Rugoconites*? sp., next to small, unidentified circular structure. Hyporelief. GSC loc. 101541. GSC 83031, ×1.



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on third fold. Outer zone smooth, with 1–2 mm wide annulus of low relief at margin. Diameter of fossil 52 mm; total relief 0·7 mm, maximum in inner disc.

*Remarks. C. plana* is distinguished by its relatively small, coarsely corrugated central disc and its large, smooth outer ring without rugosities. Unless the small concentric structure on the third ring of the central disc represents the impression of a separate, small specimen of *Cyclomedusa*, this structure could be interpreted as a bud, much like one of the Australian paratypes in which the central cone appears to be twinned. Otherwise, the fossil most closely resembling our specimen is one from the Yaryshev Formation of the Ukraine (Zaika-Novatskiy and Palij 1968, fig. 1; see also re-illustrations in Sokolov 1973, fig. 2/1, and Glaessner 1979, fig. 9/2*a*).

### *Cyclomedusa* sp.

Plate 73, fig. 1; text-fig. 5*a*

1983 *Cyclomedusa davidi?* Hofmann *et al.*, p. 455, fig. 2A, B.

*Description.* Circular to elliptical structures with numerous coarse, concentric rugae, slightly eccentric in some specimens; preserved as epi- and hyporeliefs; distinct small central tubercle (hyporelief) or pit (epirelief) at or near centre; indistinct radial markings in some specimens (e.g. Hofmann *et al.* 1983, fig. 2B); diameters 17–76 mm (N = 23, mean 38·6 mm), 0·5–3·0 mm in relief.

*Remarks.* The collection constitutes a heterogeneous lot, with specimens differing widely in quality of preservation. It includes large, flattish specimens as well as small discs with proportionately higher relief. All are characterized by moderately coarse, concentric rugae. The fifteen specimens from the 'Goz siltstone' referred to *C. davidi*? by Hofmann *et al.* (1983, p. 455) have now been determined to be epireliefs. The collection has been supplemented by several additional specimens, which include one showing a more eccentric position of the central depression, somewhat like the *C. serebrina* from the Ukraine (Palij *et al.* 1979, pl. 48, fig. 4); however, the poorly preserved marginal wrinkles do not overlap as in the Ukrainian specimen.

*Cyclomedusa* is the most cosmopolitan of the Ediacaran macrofossils (see also Wade 1972, p. 205), and most specimens have been referred to *C. davidi* Sprigg. Sun (1986) has reviewed the taxonomy of *Cyclomedusa*, restricting *C. davidi* to forms with numerous fine radial grooves on the oral surface. The scarcity of radial grooves in the specimens from the Wernecke Mountains may be taxonomically significant, or may simply reflect preservation of the aboral surface of *C. davidi*.

## Genus EDIACARIA Sprigg, 1947

*Type species. Ediacaria flindersi* Sprigg, 1947.

### *Ediacaria flindersi* Sprigg, 1947

Text-fig. 7

For synonymy up to 1966, see Glaessner and Wade 1966.

1978 *Tirasiana disciformis* Fedonkin, fig. 3, no. 6.
1979 *Ediacaria flindersi* Glaessner, p. A95, fig. 9/1.
1981 *Tirasiana disciformis* Fedonkin, p. 57, pl. 2, fig. 4.
1985*a* *Ediacaria flindersi* Fedonkin, pp. 74–75, pl. 1, figs. 2 and 5; pl. 2, fig. 4.

*Description.* Very large circular structures with tripartite organization, composed of three superimposed concentric discs, preserved as convex hyporelief. Two specimens; complete specimen (text-fig. 7) comprising inner disc 36 mm in diameter, with about 2 mm of relief, superimposed on second disc 100 mm across and about 3 mm in relief, attached to third disc 165 mm across, with about 5·5 mm of relief. Surface of innermost disc with one faint concentric circular furrow midway between its centre and its periphery; second disc with at least five distinct, narrow, unevenly spaced concentric ridges which are developed most strongly in its peripheral

TEXT-FIG. 7. *Ediacaria flindersi* Sprigg, hyporelief. GSC loc. 101532. GSC 83014, ×0·5.

portion; largest disc with faint concentric markings midway between inner and outer limits. Very faint radial markings also locally visible. Middle and outer discs with indentations that coincide with an arcuate groove which has large radius and is tangent to central disc. Part of specimen traversed by 1·0 mm-wide shrinkage crack filling. Second, incomplete specimen (GSC 83053) exhibiting inner disc 74 mm in diameter, with about 1 mm of relief, superimposed on second disc 110 mm in diameter with about 1 mm of relief attached to third disc 222 mm in diameter with about 2 mm of relief: middle disc with four concentric ridges near its periphery.

*Remarks. E. flindersi* is the largest 'medusoid' known from the Ediacara assemblage (Glaessner and Wade 1966), and the two specimens from the Wernecke Mountains are at the upper end of its known size range. Sprigg's (1947, 1949) original specimens are marked by strong radial grooves, but these are not present on the ex-umbrellar surface (Glaessner and Wade 1966; Sun 1986, p. 336). The specimens from the Wernecke Mountains are most similar to a large specimen from the Vendian of the White Sea coast, originally referred to *Tirasiana disciformis* Palij, 1976 by Fedonkin (1978, fig. 3, no. 6; 1981, pl. 2, fig. 4) but now referred to *E. flindersi* (Fedonkin 1985*a*, pl. 1, fig. 5).

Genus KULLINGIA Glaessner *in* Føyn and Glaessner, 1979

*Kullingia*? sp.

Plate 73, fig. 5

? 1979 *Kullingia concentrica* Glaessner *in* Føyn and Glaessner, pp. 39–40, fig. 8*a*.
? 1985 *Kullingia concentrica* Gureev, pp. 99–100, pl. 39, figs. 1–4.

*Description.* Two specimens from GSC locality 101543 preserved as convex discoidal hyporeliefs; figured specimen 54 mm in diameter, with about 1 mm of relief; surface smooth, provided with closely spaced, faint, regular concentric wrinkles that are most prominent near periphery; central disc 7 mm across barely noticeable; no radial pattern distinguishable; second specimen juxtaposed to first, partially preserved, about 60 mm across, with 1 mm of relief.

*Remarks.* The structures have some of the characteristics of *Kullingia*, but folds in the central portion of the discs are poorly preserved making the specimens resemble those of *Beltanelliformis*. Their larger size and more regular concentric ridges and furrows set them apart.

### Genus MEDUSINITES Glaessner and Wade, 1966

*Type species. Medusinites asteroides* (Sprigg) Glaessner and Wade, 1966.

### *Medusinites asteroides* (Sprigg), *emend.* Glaessner and Wade, 1966

Plate 73, figs. 7-9

1949 *Medusina mawsoni* Sprigg, p. 89, pl. 13, fig. 4; text-fig. 7B.
1949 *Medusina asteroides* Sprigg, p. 90, pl. 13, text-fig. 7C.
1956 *Protolyella asteroides* Harrington and Moore, p. F155, fig. 127/1.
1956 *Protolyella mawsoni* Harrington and Moore, p. F155, fig. 127/2.
1966 *Medusinites asteroides* Glaessner and Wade, pp. 605-607, pl. 94, figs. 1-5.
1968 *Medusinites asteroides* Wade, pp. 259, 260, figs. 22 and 24.
? 1973 *Medusinites patellaris* Sokolov, p. 210, fig. 3/2.
1979 *Medusinites asteroides* Glaessner, p. A94, fig. 10/1.
? 1980 *Paliella patelliformis* Fedonkin, p. 10, pl. 2, figs. 1-3.
? 1981 *Paliella patelliformis* Fedonkin, pp. 62-63, pl. 31, figs. 2 and 3; pl. 32, figs. 1 and 2.
? 1983 *Paliella patelliformis* Fedonkin, pl. 28, figs. 1, 2, 4-6.
1983 *Medusinites asteroides* Fedonkin, pl. 28, fig. 10.
? 1983 *Medusinites* sp. Fedonkin, pl. 34, fig. 1.
1985*a* *Medusinites asteroides* Fedonkin, pl. 8, fig. 2.
? 1985*a* *Medusinites* sp. Fedonkin, pl. 8, fig. 3.
? 1985*a* *Paliella patelliformis* Fedonkin, pp. 73-74, pl. 3, fig. 9; pl. 10, fig. 5.

*Description.* Subcircular convex hyporeliefs, composed of smooth central disc, separated by a subcircular groove from a broad, smooth outer ring, itself surrounded by a groove; disc one-third to one-half of diameter of whole structure. Outer diameters of three specimens 9·0, 20·5, and 25·6 mm; disc diameter respectively 4·3, 10·9, and 8·3 mm; relief respectively 0·8, 1·3, and 1·8 mm.

*Remarks.* Glaessner and Wade (1966) erected the genus *Medusinites* to include both *Medusina asteroides* Sprigg and, questionably, *M. mawsoni* Sprigg. Our three specimens, none of which shows any radial elements, most closely resemble the holotype of *M. mawsoni*, and two specimens of *Medusinites asteroides* illustrated by Glaessner and Wade (1966, pl. 97, figs. 1 and 2). Similar structures from the USSR were illustrated by Sokolov (1973, p. 210, fig. 3, no. 5) as *M. patellaris*, and as *M. asteroides* by Fedonkin (1983, pl. 28, fig. 10).

The genus *Paliella* (Fedonkin 1980, p. 10) is very close in morphology to *Medusinites*, and is said to be distinguishable from it by the presence of radial grooves in the outer zone. However, such grooves, though not dominant, are present in the type material of *Medusinites* (e.g. Sprigg 1949, text-fig. 7B, C; Glaessner and Wade 1966, pl. 97, figs. 3 and 5). Moreover, Fedonkin (1983, pl. 28, figs. 5 and 6) illustrated under *Paliella* specimens in which radial elements are not distinct. *Paliella* may thus be a junior synonym of *Medusinites*, or, if the radial pattern were considered characteristic and dominant, the structures could be referred to *Protolyella* Torell, in which case *Paliella* may be a junior synonym of *Protolyella*.

### Genus NADALINA gen. nov.

*Type species. Nadalina yukonensis* sp. nov.

*Diagnosis.* Discoidal structure of centimetric size, with large smooth inner disc separated from surrounding annular field with narrow marginal rim of small relief by a ring of numerous, equally spaced millimetric pits (as seen in epirelief); width of annulus about one-half of radius of inner disc.

*Etymology*. Named for its occurrence in the Nadaleen River map area (National Topographical Series of Canada Map 106C, 1:250,000).

### *Nadalina yukonensis* sp. nov.

Plate 73, fig. 2

*Diagnosis*. As for genus.

*Holotype*. GSC 83022.

*Etymology*. Named for its occurrence in the Yukon Territory of Canada.

*Description*. One whole specimen, preserved as elliptical epirelief on medium grey, medium-grained sandstone; 62 × 55 mm in size, with about 1 mm of relief. Disc differentiated into 2 zones, an inner flat disc without distinctive markings, 38 × 33 mm across, and an outer ring about 6–10 mm wide with less smooth surface and a 1–2 mm wide raised rim at the outer margin; between the 2 zones a partially preserved ring marked on one side of specimen by at least 9 pits, 1–3 mm wide and up to 1 mm deep, more or less regularly spaced, 5–9 mm apart. Poorly preserved partial impression of a second specimen (GSC 83015) on the same slab about 75 × 90 mm in size, with outer ring 12 mm wide, marked on inside with at least 7 pits 1–3 mm across, spaced 5–10 mm apart.

*Occurrence and type locality*. Siltstone unit 1, Section D (GSC locality 101538).

*Remarks*. The structure is unlike any known to us; we regard it as a new genus and species, and interpret it as the impression of a medusoid. The illustrated specimen is sufficiently well preserved and distinct to serve as a basis for a new taxon.

### Genus RUGOCONITES Glaessner and Wade, 1966

*Type species*. *Rugoconites enigmaticus* Glaessner and Wade, 1966.

### *Rugoconites?* sp.

Plate 73, fig. 11

*Description*. Single specimen, poorly preserved as convex hyporelief; subcircular disc 29 × 32 mm in diameter, with 2·7 mm of maximum relief; outer zone on one side of specimen with short radial furrows spaced about 3 mm apart, apparently emanating from points of bifurcation uniformly located about 5 mm from the periphery. Possible presence of ring surrounding specimen beyond margin, suggested by a diffuse, irregularly patterned, 7–9 mm wide zone.

*Remarks*. The pattern and size of the questionably bifurcating furrows are suggestive of the morphology of *Rugoconites*, of which two species have been described. The coarse furrow pattern would fit *R. enigmaticus* better than *R. tenuirugosus*, but our only specimen is so poorly preserved as to make even the identification of the genus doubtful. The genus has not before been reported from outside Australia.

### Genus SPRIGGIA Southcott, 1958

*Type species*. *Madigania annulata* Sprigg, 1949.

### *Spriggia annulata* (Sprigg, 1949) Southcott 1958

Plate 73, fig. 10

1949 *Madigania annulata* Sprigg (*partim*), pp. 93–94, pl. 16, fig. 1.
1956 *Madigania annulata* Harrington and Moore, p. F154, fig. 124.

1958 *Spriggia annulata* (Sprigg), Southcott, p. 59, fig. 3.
1979 *Cyclomedusa davidi* Føyn and Glaessner, p. 40, fig. 5*c*.
? 1981 *Cyclomedusa delicata* Fedonkin, pp. 59–60, pl. 2, fig. 2.
1984 *Spriggia annulata* Jenkins, p. 97, pl. 1, fig. 6.
? 1985*a* *Cyclomedusa delicata* Fedonkin, pp. 72–73, pl. 1, fig. 4.
1986 *Spriggia annulata* Sun, pp. 337–339, fig. 2E, fig. 5.

*Description*: Single, bipartite disc 28 mm in diameter, preserved in convex relief on a shale clast. Inner disc 17 mm in diameter, slightly convex (3 mm relief), with slightly eccentric papilla surrounded by annular rugae. Outer flange flat. Both inner disc and outer flange sculpted with numerous, submillimetric, concentric wrinkles.

*Remarks*. *Spriggia* has recently been revised by Sun (1986), who discussed its complex nomenclatural history and its distinction from similar genera. Sun regarded *Spriggia* as the impression of a fossil chondrophore.

*Spriggia wadeae* Sun, 1986

Plate 73, fig. 4

? 1979 *Cyclomedusa minuta* Fedonkin, *in* Palij *et al*., pp. 63–64, pl. 58, fig. 4.
? 1981 *Cyclomedusa minuta* Fedonkin, p. 59, pl. 4, fig. 2.
1986 *Spriggia wadeae* Sun, pp. 339–346, figs. 6A–D and 8A–C.

*Description*. Single disc preserved as convex hyporelief, 20 mm across, 0·7 mm high, with sharp outer margin and distinctly flat appearance, though sculptured by numerous annular ridges increasing in width outwards to a maximum of 1·0 mm wide. Attached to one side of specimen along about one-half of periphery, is an irregular crescentic marking 1·6 mm high, with maximum width of 10 mm, characterized by poorly defined submillimetric irregularities; shale matrix from underlying layer covering parts of disc and crescent.

*Remarks*. This structure is broadly similar to *C. minuta* from the White Sea coast (see synonymy), particularly because of the presence of the crescentic projection. However, *C. minuta* is considerably smaller and contains fewer annular ridges. The distinction between *S. wadeae* and *S. annuluta* has been discussed by Sun (1986).

Genus TIRASIANA Palij, 1976

*Type species*. *Tirasiana disciformis* Palij, 1976.

*Tirasiana* sp.

Plate 74, figs. 2 and 4

*Description*. Small discoidal hyporeliefs 10–18 mm in diameter (N = 4), 0·5–1·0 mm high, with tripartite organization: small central tubercle surrounded by inner disc that extends about halfway to periphery of whole impression; prominent circular groove separating inner disc from broad outer disc. Outer disc of specimen at bottom of Plate 74, fig. 4 bearing indistinct radial markings and narrow concentric circular groove; inner disc of specimen in Plate 74, fig. 2 with at least five circular markings of uniform size equidistant from centre, and incomplete subsidiary concentric wrinkles.

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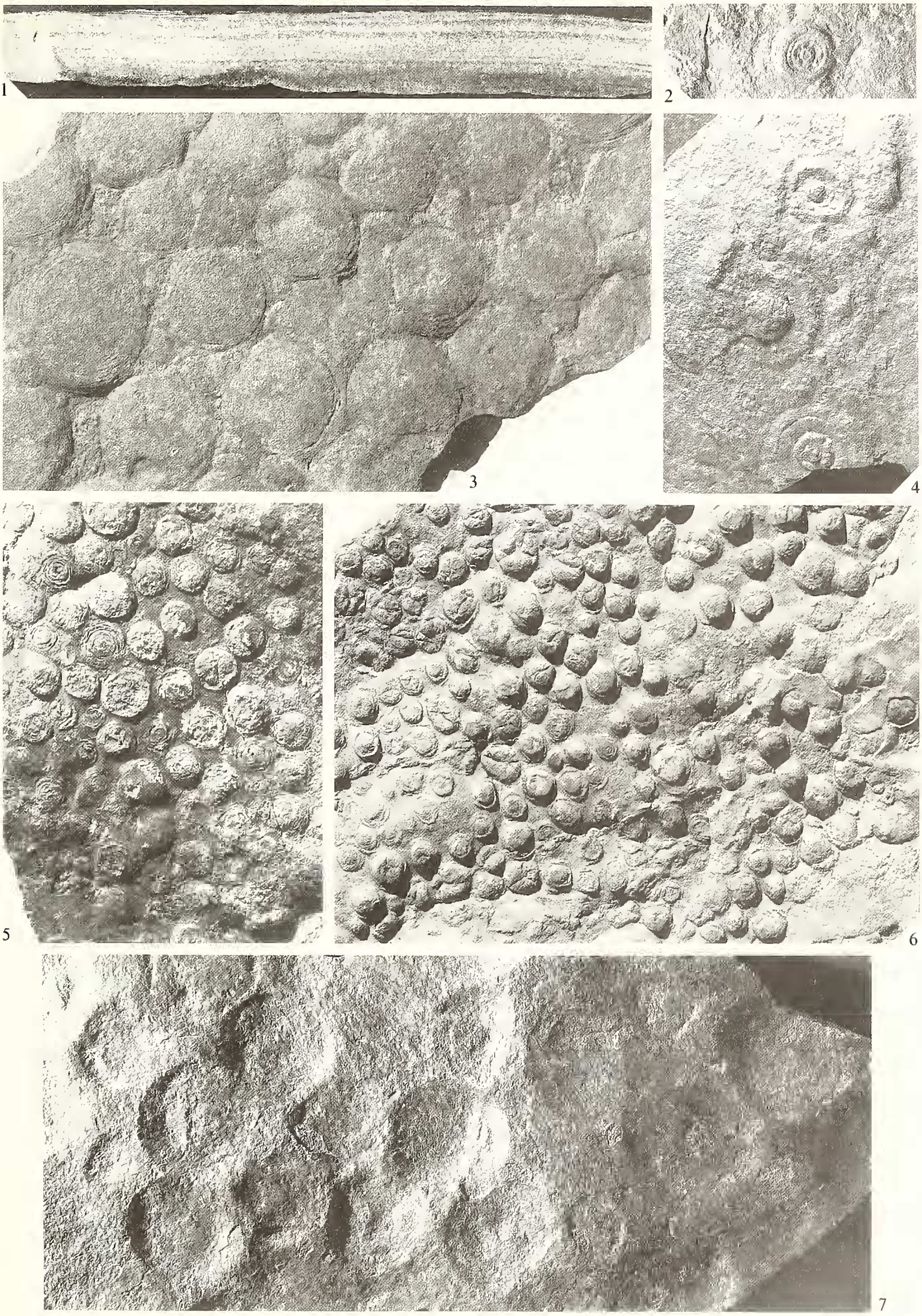
EXPLANATION OF PLATE 74

Figs. 1, 3, 5–7. *Beltanelliformis brunsae* Menner. 1, vertical section along top margin of 3. GSC loc. 101534. GSC 83032, × 1. 3, hyporelief, cluster of large specimens with smooth centres. 5, hyporelief; cluster of specimens with concentric wrinkles in central parts of discs. GSC loc. 99094. GSC 83035, × 1. 6, hyporelief; cluster of small specimens with high relief cast in underlying shale. GSC loc. 101541. GSC 83036, × 1. 7, epirelief; cluster of large specimens with low relief on underlying sandstone. GSC loc. 101532. GSC 83037, × 1.

Figs. 2 and 4. *Tirasiana* sp., hyporeliefs. 2, GSC loc. 99042. GSC 83033, × 1. 4, GSC loc. 101531. GSC 83034, × 1.



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*Remarks.* The specimens are very similar to a slightly larger specimen of *Tirasiana* sp. from the Yaryshev Formation in the Ukraine illustrated by Palij *et al.* (1979, pl. 49, fig. 7), which also has circular markings in the middle ring surrounding the central tubercle, like the specimen in Plate 74, fig. 4. The specimen in Plate 74, fig. 2 resembles *Protoniobia* Sprigg, 1949 (pl. 9, fig. 1) but lacks the marginal subcircular structures. *Protoniobia* was regarded as a concretion by Cloud (1968), and was treated as a 'rejected and unrecognizable' taxon by Glaessner (1979, pp. A112–A113), but we regard our specimen as organic.

Phylum uncertain

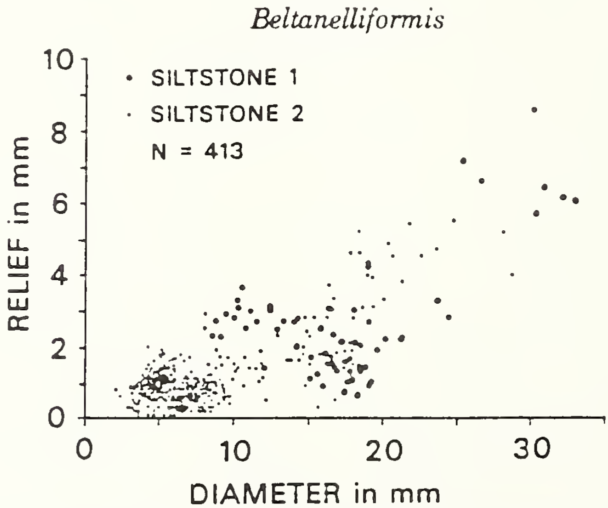
Genus BELTANELLIFORMIS Menner, in Keller *et al.* 1974

*Type species. Beltanelliformis brunsae* Menner, in Keller *et al.* 1974.

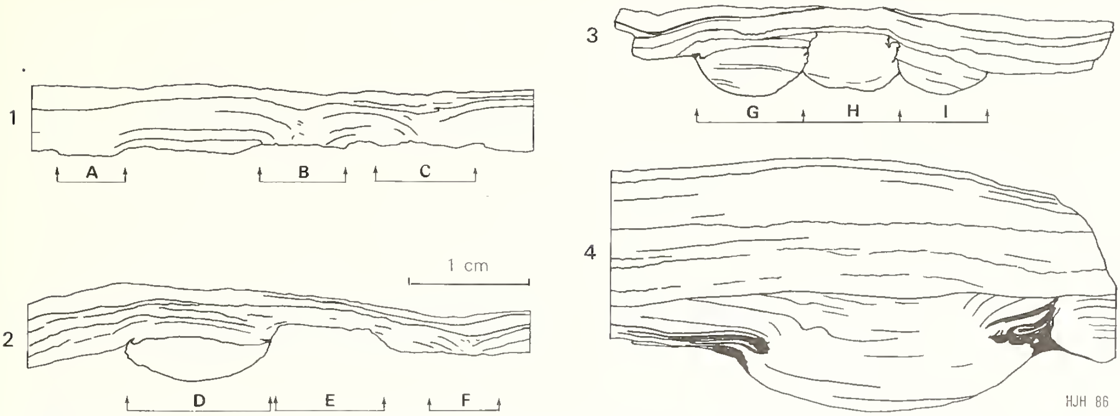
*Beltanelliformis brunsae* Menner, in Keller *et al.* 1974

Plate 74, figs. 1, 3, 5–7; Plate 75, figs. 1–8; text-figs. 8 and 9

? 1969 'minute fossils' Wade, pl. 69, fig. 7.
1974 *Beltanelliformis brunsae* Menner, *in* Keller *et al.*, p. 132, pl. 1, fig. 10.
1976 *Nemiana simplex* Palij, pp. 70–71, pl. 21, fig. 5; pl. 22, figs. 1–3.
1979 *Nemiana simplex* Palij *et al.*, p. 64, pl. 49, figs. 1, 5, 6.
1981 *Beltanelliformis brunsae* Fedonkin, p. 58, pl. 1, figs. 1–6.
1981 *Nemiana simplex* Fedonkin, p. 57, pl. 3, figs. 2 and 9.
1981 *?Sekwia excentrica* Hofmann, fig. 4H.
1983 *Beltanelliformis brunsae* Hofmann *et al.*, p. 455, fig. 1C.
1985 *Beltanelloides simplex* (Palij) Gureev, pp. 97–98, pls. 35, 36, 37, figs. 1–4, 7; pl. 38, fig. 1.
1985*a* *Beltanelliformis brunsae* Fedonkin, pp. 70–71, pl. 5, fig. 2.
1985*a* *Nemiana simplex* Fedonkin, p. 70, pl. 5, fig. 3.
1985 *Nemiana simplex* Bekker, pl. 29, fig. 6.




TEXT-FIG. 8. Size variation of *Beltanelliformis brunsae* Menner from the Wernecke Mountains.




TEXT-FIG. 9. Vertical sections of *Beltanelliformis brunsae*. 1 corresponds to Plate 75, fig. 1. 2 to Plate 75, fig. 2. 3 is a tracing from a thin section cut across the three aligned specimens at right margin of Plate 75, fig. 3. 4 is a tracing from a thin section cut parallel to the large specimen illustrated in Plate 75, fig. 4.

*Description.* Flat to button-shaped, circular to subcircular convex hyporeliefs and concave epireliefs; less commonly, concave hyporeliefs and full reliefs; 2·2–33·1 mm across; (mean diameter = 9·15 mm; s = 5·88 mm; N = 413); 0·1–8·5 mm in relief (mean relief = 1·35 mm; s = 1·21 mm; N = 413); specimens in Siltstone unit 1 generally larger than those in Siltstone unit 2 (text-fig. 8). Individuals typically very closely crowded, with pronounced unimodal size distribution for specimens on individual bedding planes. Specimens with high relief (diameter/relief < 10) smooth, or provided with one or more curvilinear, irregularly linear, bifurcating, or star-shaped furrows or folds. Specimens of low relief (diameter/relief > 10) with narrow concentric peripheral wrinkles or folds, and smooth central field; some vertical sections showing collapsed sediment immediately above disc (e.g. Pl. 75, figs. 1–3; text-figs. 9.1; 9.2, specimen F); all gradations between low- and high-relief specimens present (text-fig. 8). Vertical sections of complete, high-relief specimens exhibiting lenticular nature, with semicircular bottom, deformed upper semicircle, and involuted sides; internal sediment fill laminated, graded, massive, or exhibiting slump structures (text-figs. 9.2, specimen D; 9.3; 9.4). Rare concave hyporeliefs hemispheroidal with central circular marking (e.g. Pl. 75, fig. 5) to relatively flat and wrinkled. Concave epireliefs shallow and relatively smooth, or with irregular, partly concentric wrinkles. Specimens preserved in full relief subspherical, with circular marking on top (Pl. 75, figs 6 and 7).

*Remarks.* The discs here assigned to *B. brunsae* are the most common fossils in the Wernecke assemblage. They typically are closely crowded, and the size distribution of specimens on individual bedding planes is strongly unimodal, indicating that each sample represents a population of individuals at the same stage of ontogenetic development assembled on a mud substrate, before the arrival of storm-deposited sand.

The Wernecke specimens are similar to forms described from the Russian Platform under a variety of names (see synonymy). The size range of typical '*Nemiana simplex*' from the Ukraine is reported to be 2–60 mm (Palij 1976, p. 70; Gureev 1985, p. 97). Our specimens are mainly at the lower end of the size range for this form, and are more similar to the '*N. simplex*' from the White Sea coast (Fedonkin 1981, p. 57, pl. 3, figs. 2 and 9), for which diameters are between 10 and 30 mm and the relief is 0–3 mm. Specimens from the Soviet Union also exhibit a single circular marking on their upper surface which Fedonkin (1985*a*) interpreted as an oral opening. Taxonomic assignment and interpretation of the discs from the Soviet Union is difficult because, despite an abundance of photographic illustrations of the basal surface, little has been documented of their internal structure.

The Wernecke discs show considerable variation in preservation from one bedding plane to another, ranging from smooth, flat discs with numerous delicate marginal wrinkles (= *B. brunsae* Menner) to more strongly convex forms with fewer and coarser, more irregular wrinkles, some of which extend into the central parts of the disc (= *N. simplex* Palij). This morphological transition indicates to us that *Beltanelliformis* and *Nemiana* are best explained as preservational variants of a single globular biological taxon.

Any interpretation of *Beltanelliformis* must account for: (1) the concentric wrinkling; (2) the variety of sedimentary fills and structures in and above the fossils (text-fig. 9; Pl. 74, fig. 1; Pl. 75, figs. 1, 2, 4); and (3) the complete gradation between *Beltanelliformis*-type and *Nemiana*-type preservation (text-fig. 8). We propose that *Beltanelliformis*-type forms were preserved where globular bodies resting on the mud substrate, either as single spheroidal organisms, or, less likely, as spheroidal colonies comparable to those figured by Glaessner (1969, fig. 3), were buried by storm-deposited sand. If, upon burial, the bodies quickly collapsed, undisturbed lamination would be preserved above the locus of these bodies (e.g. Pl. 74, fig. 1). If the bodies maintained their integrity long enough to allow the accumulation of sand around and above them subsequent decay of the spheroids would have produced the collapse of the sand into the space previously occupied by the bodies, resulting in the disturbed lamination now encountered above some of the specimens (text-figs. 9.1; 9.2, specimen F). In contrast, specimens exhibiting, *Nemiana*-type preservation probably were partially buried in the mud, most likely as a result of slow accumulation of mud around the bases of the spheroidal organisms. As a consequence of rapid, storm-induced burial, some specimens were filled with graded to parallel laminated sand (text-figs. 9.2, specimen D; 9.3). Other specimens remained unfilled, and subsequent collapse of the organism produced disturbed (slumped) lamination (text-fig. 9.4). Folding of the tough outer wall of the organism during rapid burial probably produced the concentric to irregular wrinkles visible on most specimens of *Beltanelliformis* and '*Nemiana*'.

Lithology also appears to have played an important role in determining the mode of preservation. Gureev (1985) has pointed out that, in the Ukraine, *Beltanelloides sorichevae* (*Beltanelliformis*-type preservation) occurs predominantly in shale, whereas '*Beltanelloides simplex*' (*Nemiana*-type preservation) occurs predominantly in siltstone and sandstone. Based on this, Gureev (1985) suggested that the two forms might be synonymous. Our specimens further support this hypothesis. In the Wernecke biota, the best examples of *Beltanelliformis*-type preservation (e.g. Pl. 74, fig. 2) are cast by argillaceous siltstone, whereas the best examples of *Nemiana*-type preservation (e.g. Pl. 75, figs. 5–8) are cast by sandstone.

Some specimens of *Beltanelliformis* exhibiting *Nemiana*-type preservation superficially resemble hemispherical anemone burrows such as *Bergaueria* Prantl, 1945. Palij *et al.* (1979) pointed out that '*Nemiana*' can be distinguished from *Bergaueria* by the presence of numerous wrinkles and folds resulting from deformation of a soft-bodied organism following burial, the consistent absence of an overlying vertical cylinder, and by the fact that adjacent specimens deform but do not cross-cut each other. The sporadic occurrence of specimens preserved in concave hyporelief (Pl. 75, fig. 5) in the Wernecke assemblage further suggests that *Beltanelliformis* represents the impression of a soft-bodied organism rather than a hemispherical burrow-fill. Hemispherical specimens of *Beltanelliformis* also superficially resemble the base of the Cambrian–Ordovician fossil *Protolyella* Torell 1870, which Seilacher (1984) has interpreted as the internal sandy skeleton of an anemone. However, *Protolyella* exhibits concentric hemispherical sediment fill reflecting active packing by the organism, whereas hemispherical *Beltanelliformis* were passively filled with graded, laminated, or massive sediment.

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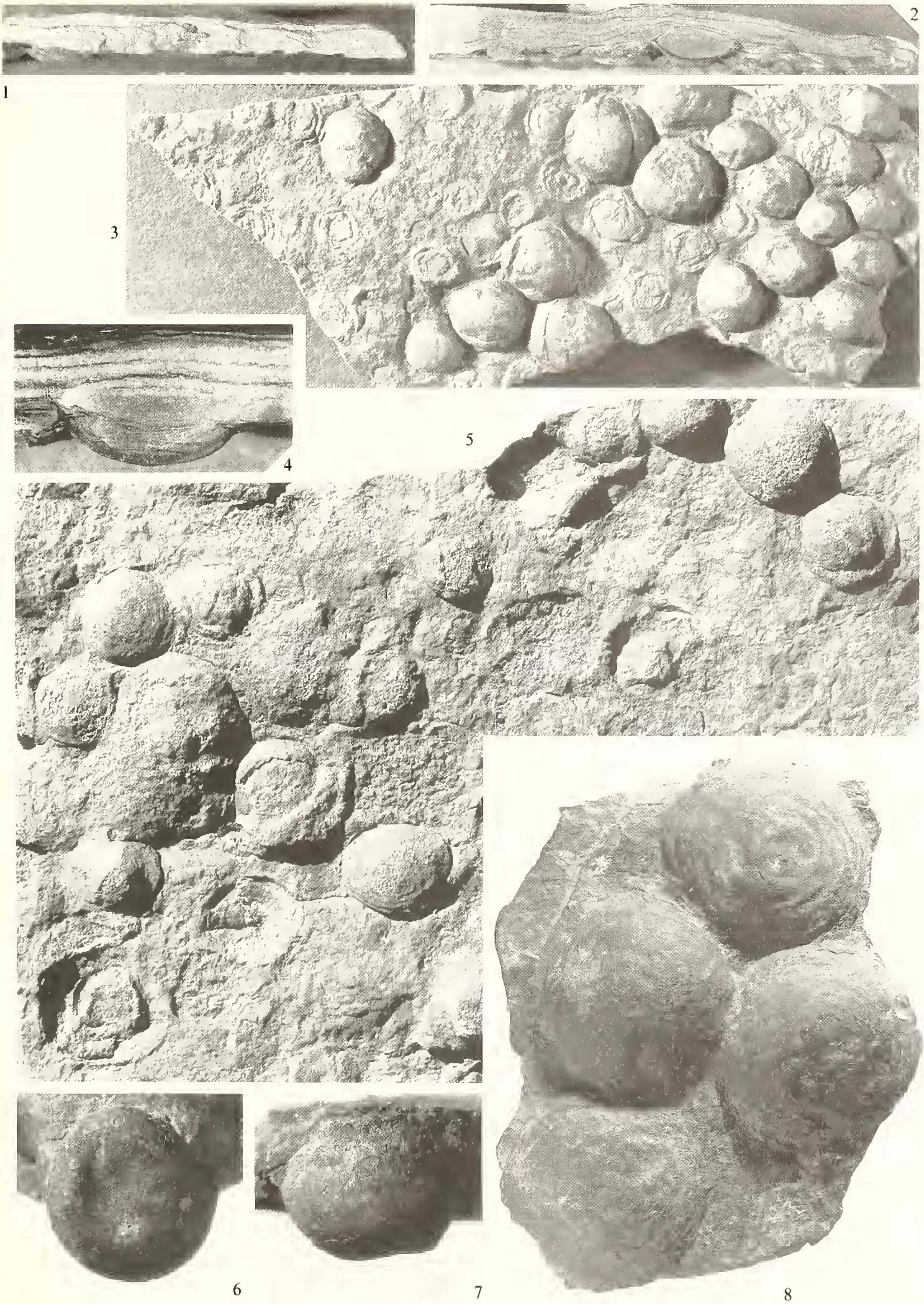
EXPLANATION OF PLATE 75

Figs. 1–8. *Beltanelliformis brunsae* Menner. 1, vertical section along inclined left margin of specimen in fig. 3, showing sagged laminae above specimens of *Beltanelliformis*. 2, vertical section along upper right margin of fig. 3, showing draping of laminae over specimens, ×1. 3, lower surface, showing close association of high relief (GSC 83038) and low relief (GSC 83039) forms. GSC loc. 101532. 4, vertical section showing laminated fill and slight draping of large specimen. GSC loc. 101531. GSC 83040, ×1. 5, cluster with specimens in both convex and concave hyporelief. GSC loc. 99095. GSC 83041, ×0·7. 6, bedding plane view of specimen preserved in full relief. GSC loc. 99036, GSC 83042, ×2. 7, side view of specimen in fig. 6, ×2. 8, largest observed specimens in the Wernecke assemblage. GSC loc. 101531. GSC 83043, ×1.




NARBONNE and HOFMANN, *Beltanelliformis*

Nevertheless, *Beltanelliformis*, *Bergaueria*, and *Protolyella* can be closely similar in plan view, and can only be distinguished through study of their three dimensional form and the nature of their internal sediment.

*Beltanelliformis brunsae* was originally regarded as a medusoid (e.g. Sokolov 1972*a*, *b*; Menner 1974; Palij *et al.* 1979; Fedonkin 1981). However, Sokolov (1976), Sokolov and Fedonkin (1984, p. 13), and Glaessner (1984, pp. 24–25) who use the designation *Beltanelloides sorichevae* for such structures, later related them to *Chuaria*-like organisms, which are typically preserved as carbonaceous compressions. A lack of associated carbonaceous material, the apparent presence of a circular aperture on the upper surface, and the centimetric size of some specimens, makes the comparison of *Beltanelliformis* with chuariamorphids tenuous. Neither *Beltanelliformis* nor *Beltanelloides* appear in the *Treatise* (Glaessner 1979), and we have not had the opportunity to compare type material of these two taxa. The former may be an objective synonym (ICZN 1964, Art. 61*b*), however, because of the possible distinctness of specimens referred to *B. sorichevae* Sokolov (1972*a*, pl. 4, figs. 4–8), which have no circular impressions in the centre, and to *Beltanelliformis brunsae* Menner (Sokolov 1972*a*, pl. 4, fig. 2), and the apparent questionable nomenclatural status of the former (no holotype designated for species from among two 'forms'; no diagnosis given; ICZN 1964, Art. 13*a* (i), 15, 45*b*, *e*, 72*a*), we have assigned our structures to the validly published taxon *Beltanelliformis*.

## ICHNOFOSSILS

### Ichnogenus GORDIA Emmons, 1844

*Type ichnospecies. Gordia marina* Emmons, 1844.

### *Gordia marina* Emmons, 1844

Text-fig. 10*a*

? 1976 'crawling trails', Palij, pl. 26, figs. 1 and 2.
? 1979 'crawling trails, first variety', Palij *et al.*, p. 77, pl. 53, figs. 2 and 4.
? 1981 *Gordia* sp., Hofmann, p. 309, fig. 5*b*.
1983 *Gordia* sp., Fritz *et al.*, pl. 44.1, fig. 3.
? 1985*b* *Gordia* sp., Fedonkin, pl. 23, fig. 1.

*Description.* Two specimens, preserved as concave epireliefs and convex hyporeliefs on very thin beds of fine-grained sandstone. Burrows horizontal and irregularly meandering; true branching absent, but cross-overs present. Burrows smooth with a diameter of approximately 1 mm. Burrow fill similar to host lithology.

*Remarks.* The presence of numerous cross-overs is commonly used to distinguish *Gordia* from slender specimens of *Planolites* and *Helminthopsis* (Książiewicz 1977, p. 155). This criterion, based on Phanerozoic specimens, appears to be less significant in the Ediacaran, where forms transitional between *Gordia* and *Planolites* are common (e.g. text-fig. 10*b*; Glaessner 1969, fig. 5B; Palij *et al.* 1979, pl. 53, figs. 2 and 4). Książiewicz (1977) and Crimes and Anderson (1985) recognized three ichnospecies of *Gordia*: *G. marina* Emmons, *G. molassica* (Heer 1865), and *G. arcuata* Książiewicz 1977, but we agree with Pickerill (1981) that *G. molassica* is indistinguishable from *G. marina*.

*Gordia* occurs widely in Phanerozoic strata and is one of the most commonly reported Ediacaran ichnofossils. *G. marina* occurs on the Russian Platform and in northwestern Canada, *G. arcuata* has

TEXT-FIG. 10. *a*, *Gordia marina* Emmons, concave epirelief. GSC loc. 101533. GSC 83044, ×1. *b*, *Planolites montanus* Richter, hyporelief. GSC loc. 101531. GSC 83045, ×1. *c*, *Neonereites*? sp., hyporelief. GSC loc. 101533. GSC 83046, ×1. *d*, *P. montanus* Richter, hyporelief. GSC loc. 101532. GSC 83047, ×1. *e*, horizontal backfilled burrow, ?epirelief. GSC loc. 101532. GSC 83048, ×1. *f*, Dubiofossil A, probably epirelief. GSC loc. 101536. GSC 83049, ×1. *g*, *Vendotaenia*? sp. GSC loc. 101540. GSC 83050, ×2. *h*, Dubiofossil B. GSC loc. 101532. GSC 83051, ×1. *i*, Dubiofossil C. GSC loc. 101541. GSC 83052, ×1.


a
b
c
d
e
f
g
h
i

been reported from northern British Columbia (Fritz and Crimes 1985), and *Gordia* sp. occurs in the Ediacaran of Australia (Glaessner 1969, fig. 5*b*), the Russian Platform (Palij *et al.* 1979), the Mackenzie Mountains (Hofmann 1981), and Newfoundland (Crimes and Anderson 1985). *Gordia* probably represents the crawling or feeding burrow of a worm-like organism (Chamberlain 1977).

### Ichnogenus NEONEREITES Seilacher, 1960

*Type ichnospecies. Neonereites biserialis* Seilacher, 1960.

### *Neonereites*? sp.

Text-fig. 10*c*

*Description.* Four specimens occurring in convex hyporelief on thinly bedded, fine-grained sandstone. Burrows slightly to moderately sinuous, up to 90 mm long, each consisting of a uniserial string of spherical to slightly ellipsoidal pellets 3–5 mm in diameter; pellets locally in contact, but typically irregularly spaced up to 5 mm apart; pellets composed of well-sorted sand.

*Remarks.* Specimens closely resemble those figured by Fritz and Crimes (1985, pl. 3*f*) from the Ediacaran of northern British Columbia. Among described species of *Neonereites*, they most closely resemble *N. uniserialis* Seilacher, but differ in that the pellets are irregularly spaced. *N. uniserialis* has been reported from the Vendian of the Russian Platform (Fedonkin 1977; Palij *et al.* 1979) and is common in Phanerozoic deposits (Häntzschel 1975). *Neonereites* probably represents the feeding burrow of a worm-like organism, most likely an annelid (Hakes 1976).

### Ichnogenus PLANOLITES Nicholson, 1873

*Type ichnospecies. Planolites vulgaris* Nicholson and Hinde, 1875.

### *Planolites montanus* Richter, 1937

Text-fig. 10*b*, *d*

1970 'hypichnial and exichnial casts', Banks, p. 26, pl. 1*b*, *d*.
? 1970 'curved trails', Webby, p. 87, fig. 3*d*.
1970 *Planolites ballandus* Webby, p. 95, fig. 14A–C.
1973 'hypichnial and endichnial burrows', Banks, p. 4, fig. 4*a*.
1977 *Planolites* sp., Fedonkin, p. 184, pl. 2*d*.
1979 'crawling traces, third variety', Palij *et al.*, pp. 77–78, pl. 54, fig. 2.
1979 *Planolites* cf. *serpens*, Palij *et al.*, p. 73, pl. 42, fig. 6.
1984 *Planolites* sp. Glaessner, p. 70, fig. 2/7.
1985*b* *Planolites* cf. *serpens* Fedonkin, pl. 28, figs. 3, 6.

*Description.* Specimens occurring in convex hyporelief and concave epirelief on very thin beds of siltstone and fine-grained sandstone. Burrows highly sinuous and undulatory, occurring on bedding surfaces as small knobs and discontinuous, curved, burrow segments. Burrows cylindrical, with diameters ranging from 0·4 to 1·2 mm (N = 100); indistinct, irregularly spaced constrictions giving burrows a faint 'pinch-and-swell' appearance. True branching and cross-overs of adjacent specimens rare. Burrow fill structureless, and differing from host lithology.

*Remarks.* The taxonomy of *Planolites* has recently been reviewed by Pemberton and Frey (1982), who concluded that *Planolites* can be distinguished from the morphologically similar burrow *Palaeophycus* Hall by the presence of processed burrow-fill and the absence of a burrow lining in *Planolites*. Many specimens of *P. montanus*, including the ones in this study, exhibit a faint 'pinch-and-swell' appearance reminiscent of *Torrowangea* Webby, 1970. However, the swellings in *Torrowangea* are well defined and evidently represent a back-fill structure (Webby 1970), whereas the swellings in *P. montanus* are poorly defined and apparently reflect the undulose nature of the burrow. The typically meandering pattern of *Torrowangea* also differs from the sinuous to undulose pattern of *P. montanus*.

*P. montanus* is very common in the Wernecke assemblage, a feature typical of many Ediacaran assemblages (see synonymy above). *P. montanus* also occurs commonly throughout the Phanerozoic (Pemberton and Frey 1982). *Planolites* probably represents the feeding burrow of a vermiform organism (Pemberton and Frey 1982).

## BACK-FILLED BURROW

Text-fig. 10*e*

*Description.* Single, fragmentary specimen on the (?)upper surface of a very thin bed of argillaceous, fine-grained sandstone. Specimen a gently curved, partially compressed cylinder 11 mm wide and at least 17 mm long; with well-developed back-fill.

*Remarks.* Although its fragmentary nature precludes definite identification, the specimen exhibits a back-fill structure similar to *Muensteria* von Sternberg 1833 or *Beaconites* Vialov 1962. Similar traces occur in the Ediacaran of Australia (R. J. F. Jenkins, written comm. 1986).

## METAPHYTES

### Group VENDOTAENIDES Gnilovskaya, 1971
### Genus VENDOTAENIA Gnilovskaya, 1971

*Type species. Vendotaenia antiqua* Gnilovskaya, 1971.

### *Vendotaenia*? sp.

Text-fig. 10*g*

*Description.* Isolated, smooth carbonaceous ribbons, curved and bent, 0·4–2·0 mm wide, largest fragment of nine specimens seen 30 mm long; faint, submillimetric longitudinal striae present in portions of filament.

*Remarks.* The ribbons have an appearance intermediate between those referred to *Vendotaenia* and *Tyrasotaenia* from the Russian Platform. The broad diameter, the curved nature, and the faint microscopic longitudinal striae suggest affinity with *Vendotaenia*, whereas twisted specimens bear more resemblance to *Tyrasotaenia*. However, longitudinal striae have also been reported for the latter genus, though these have been ascribed to folding of the thallus.

## DUBIOFOSSILS

### Dubiofossil A

Text-fig. 10*f*

*Description.* Almost complete, flat, gibbous disk, 40 × 29 mm, with marginal groove 0·8 mm deep; margin on one side almost rectilinear for about 17 mm, remainder evenly curved. No further identifiable markings.

*Remarks.* The specimen has no diagnostic features which would allow it to be classified. Possibly, it represents a severely distorted *Cyclomedusa*, though the absence of concentric wrinkling is against such an interpretation.

### Dubiofossil B

Text-fig. 10*h*

*Description.* Single specimen preserved in convex hyporelief, 39 × 28 mm; subhexagonal, with outer rim 1·2–4·5 mm wide and 0·5–1·2 mm high. Trapezoidal ridge 15 × 12–19 mm and up to 2·0 mm high near centre of specimen. Faint parallel ridges approximately 1·0 mm apart locally preserved on central trapezoid and outer rim.

*Remarks*. The hexagonal outline and central trapezoid are both features that have not previously been described from Ediacaran macrofossils. The specimen appears to have been flattened, and consequently it is difficult to determine whether these represent primary features. Patterns such as those exhibited by dubiofossil B occur commonly on much smaller compressed leiospherid microfossils (e.g. Timofeev 1969), and it is possible that our specimen represents a large, compressed, spheroidal or sac-shaped organism.

### Dubiofossil C

Text-fig. 10*i*

*Description*. Large number of minute pits, preserved on the upper surface of an olive-grey weathering siltstone lamina; diameters 0·5–1·2 mm, relief about 0·1 mm; specimens scattered, generally not contiguous. Similar, but smaller depressions exposed in one corner of the slab 1·0 mm below the first layer.

*Remarks*. The pits do not appear to be moulds of sand grains, inasmuch as the overlying sediment of coarse siltstone/very fine sandstone is, within some pits as well as outside them, still attached to the epirelief surface and does not contain coarse sand grains. Because of their small size and the inferred subtidal setting of the sediment, they do not appear to be rainprints. We thus consider it possible that they are fossils; they may represent an assemblage of juvenile forms of *Beltanelliformis* or *Bergaueria*. Alternatively, they resemble small pits associated with some specimens attributed to *Arumberia* (e.g. Bland 1984, figs. 1*b* and 2*b*, *c*), which differ, however, by the presence of superimposed fine, parallel to subparallel narrow ridges and wider grooves.

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